THE LONG-TERM EFFECTS OF FIRE ON FOREST ANT COMMUNITIES: MANAGEMENT IMPLICATIONS FOR THE CONSERVATION OF BIODIVERSITY

ALAN YORK

The long-term impact of fire as an agent of habitat disturbance affecting ant communities was studied in a coastal forest environment. A chronosequence approach utilising sites with understoreys aged between 2 and 14 years post-fire found that ant communities decreased in species richness with time since fire. Data from a control site monitored for 7 years after fire showed similar trends. A substantial proportion of the forests' overall ant richness is, however, contributed by 'rare' species, which are distributed across the full range of forest understorey age classes. Positive management through the prevention of frequent fires and the maintenance of habitat mosaics is required in this area to ensure the conservation of species and the maintenance of biodiversity. ☐*Ants, fire, biodiversity, conservation, management, Myall Lakes, New South Wales, Australia.*

Alan York, School of Biological Sciences, University of New South Wales, PO Box 1, Kensington, N.S.W. 2033, Australia; present address: Research Division, State Forests of New South Wales, PO Box 100, Beecroft N.S.W. 2119, Australia; 21 September 1993.

Within natural ecosystems, equilibrium and homogeneity exist only as average conditions on a large spatial and temporal scale. Disturbance is both a major source of heterogeneity in the structure and dynamics of natural communities and an agent of selection in the evolution of life histories (Sousa, 1984). Fire is clearly an agent of disturbance within Australian forest ecosystems, although, as a recurrent component, it has contributed to their development, with highly evolved adaptations exhibited by the flora and fauna. Because eucalypts have characteristics that give good recovery after light to moderate fires, low intensity fires are commonly used as a management tool to reduce the risk of destructive wildfire. In forest environments, a variety of fire 'prescriptions' are used to protect timber resources, promote regeneration, and maintain the diversity of species and habitats (see Underwood et al., 1985; Buckley, 1992).

The aim of this study was to investigate the long-term effect of fire on the richness of forest ant communities. In a management context, an assessment of species richness offers an easily applied method that can establish a base-line from which departures in composition or species abundance can be measured (Main, 1992). It also provides a means of comparing the conservation 'value' of different areas and assessing the impact of management strategies.

There is good theoretical, and growing empirical evidence to support the role of biological diversity in the maintenance of ecological processes within forests (see Woodward, 1993). This has translated into a growing awareness of the role played by invertebrate groups (both directly and indirectly) in the maintenance of productivity within ecosystems. This has led increasingly to the inclusion of invertebrate conservation strategies within environmental management policies. In addition, because of their abundance and functional importance, certain arthropod groups have a sensitivity and responsiveness to system structure that makes them useful indicators of environmental status and condition (Mattson, 1977). Ants in Australia are ubiquitous, abundant and highly active. They are one of the most important animal groups in terms of energy flow (Brown & Taylor, 1970; Rogers et al., 1972) and the diversity and structure of ant communities is often correlated with the composition of other components of the invertebrate fauna (Majer, 1983). Thus, they are increasingly being used as bio-indicators in a management context (Yeatman & Greenslade, 1980; Majer et al., 1984; Andersen & McKaige, 1987; Burbidge et al., 1992).

METHODS

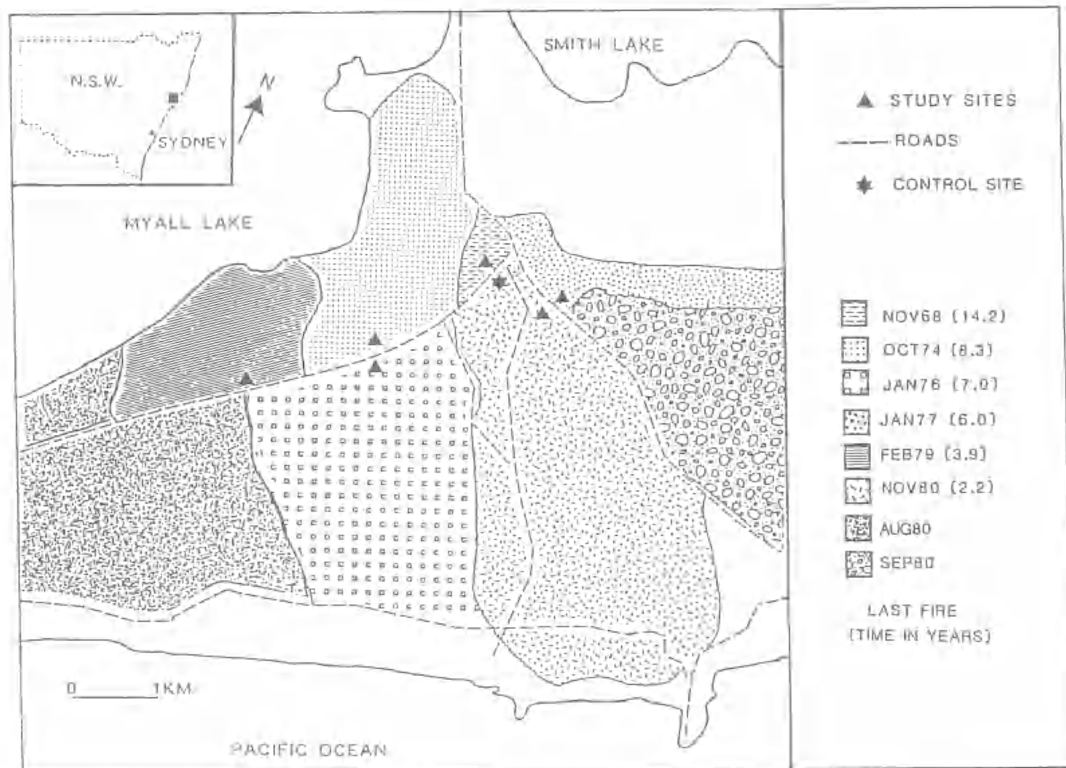The study was conducted in Myall Lakes National Park on the mid-north coast of New South

FIG. 1. Location of study sites within fire-induced habitat mosaic, Myall Lakes National Park, N.S.W.

Wales (32°26'S, 152°32'E) about 300km to the north of Sydney. The study area is isolated from adjacent habitats by two coastal lakes, Myall and Smith (Fig. 1), and is recognised as a single Land System due to its homogeneity (Myerscough & Carolin, 1986). The transgressive dunes support mainly open forest (averaging 26m in height with a projected foliage cover of 62%) with *Eucalyptus pilularis* and *Angophora costata* as dominants. The forest understorey is a rich mixture of sclerophyllous shrubs (Fox, 1981) whose height is a function of time since fire (Fox et al., 1979). The forest was extensively burnt during an intense wildfire in 1968, and has subsequently experienced a high frequency of low-intensity fires, usually during spring and summer. At the time of this study, active fire management by the National Parks and Wildlife Service of New South Wales had resulted in a mosaic of post-fire successional stages within the area, with forest understorey patches ranging from 2.2 to 14.2 years post fire (Fig. 1). The 'natural' fire interval has been estimated as 5-15 years in these forests (Walker, 1981; Fox & Fox, 1986), although increased human usage has shortened this interval considerably in many areas.

The high fire frequency precluded monitoring of a single site and its fauna (particularly under replicate conditions) over a long time period. In this study, the hypotheses that ant species richness does not change in the long term after fire was tested using a chronosequence approach, verified by the monitoring of a control site over time. In order to best approximate a 'time since fire' sequence, a number of study plots were selected so as to minimise non-temporal differences between sites. Plots could be accurately allocated to age classes as detailed fire records had been kept since 1968. Within each understorey age, a 1ha plot was subjectively selected so as to best typify that habitat type, and 4 sub-plots randomly established. Plots had experienced similar fire frequencies and season of burn, had low slope angles (0-11°) and predominantly north-east to south-east aspects. The use of a large-scale 'natural' experiment such as this prevented effective spatial replication (see Hurlbert, 1984), therefore plots were chosen so that sub-plots reflected the variation apparent at a larger scale within each age class. As part of a related study (see York, 1989), a control site was established and monitored for 6

Site code	Time since last fire (years)	Replicate values (9 pitfalls open for 7 days)				Site values Mean (S.E.)
NOV80	2.2	16	18	21	20	18.8 (1.1)
FEB79	3.9	15	14	18	18	16.3 (1.0)
JAN77	6.0	18	13	10	16	14.3 (1.8)
JAN76	7.0	15	10	13	13	12.8 (1.0)
OCT74	8.3	11	11	12	6	10.0 (1.4)
NOV68	14.2	7	9	8	11	8.8 (1.1)

Time since last fire (years)	Replicate values (9 pitfalls open for 7 days)				Site values Mean (S.E.)
1.1	17	17	19	19	18.0 (0.6)
2.2	19	16	17	15	16.8 (0.9)
3.2	17	17	13	17	16.0 (1.0)
4.2	15	13	14	13	13.8 (0.5)
5.2	16	15	16	18	16.3 (0.6)
6.2	16	14	17	16	15.8 (0.6)
7.2	10	12	14	16	13.0 (1.3)

TABLE 1. Ant species richness on plots differing in time since last fire: Above, chronosequence values; Below, control site values.

years, yielding data from 1.1 to 7.2 years after fire.

Ants (and other epigaeic invertebrates) were sampled at each sub-plot using 9 pitfall traps arranged within a 10m × 10m grid. Traps were 2.5 × 15cm Pyrex test tubes fitted in plastic sleeves and sunk flush with the soil surface (after Majer, 1978). The pitfall traps contained 20ml of 70% alcohol (and a few drops of glycerol) and were left open for 7 days during fine weather. For the chronosequence component, sampling was conducted in early February 1983; while sampling at the control site was conducted each February from 1982 to 1988. Samples were returned to the laboratory and examined with a binocular microscope where ants were identified to genus using the key published in Greenslade (1979). A reference collection was established, and final verification of species completed at the National Insect Collection in the CSIRO, Division of Entomology, Canberra. All analytical procedures were performed using the SPSSX statistical package (SPSS Inc., 1983) on the VAX 11-785 computing facilities at the University of New South Wales. Data from the 'chronosequence' and 'control' sites were analysed separately, with regression coefficients from linear regression models compared using the procedure described by Steel & Torrie (1981).

RESULTS

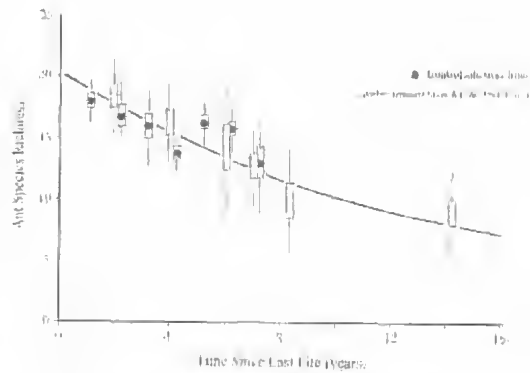In excess of 25,000 individuals from 41 ant species were caught and identified during this

FIG. 2. Changes in ant species richness with time since last fire.

study. These represent primarily surface-active species as certain hypogaeic ants species found by regular soil and litter survey may not be caught in pitfall traps (Majer, 1982). Analysis of the chronosequence data revealed that mean values of ant species richness varied from 8.8 to 18.8, with comparable levels of variability between forest understorey age classes (Table 1). A one-way analysis of variance procedure suggested that ant species richness differed significantly between sites of different ages since fire ($F=9.50$ $DF=5,18$ $P=0.0001$). Scheffe's multiple-comparison test (Steel & Torrie, 1981) indicated that means of sites closest in age were most similar, with an overall pattern as follows:

TIME SINCE LAST FIRE (years) 2.2 3.9 6.0 7.0 8.3 14.2
MEAN RICHNESS VALUE 18.8 16.3 14.3 12.8 10.0 8.8

(Lines represent means not significantly different at 5% level).

Using regression procedures it was found that there was a significant relationship between ant species richness and time since last fire. Sixty-one percent of the variance in ant species richness was explained by time in the following exponential regression model (see Fig. 2):

ANT SPECIES RICHNESS $= 20.34\, e^{-0.067\,\text{(YEARS SINCE FIRE)}}$

$r = -0.781$ $r^2 = 60.9\%$ $n = 24$ $P < 0.001$

Although a linear model explained a similar amount of variance (62.8%), it has the limitation of more rapidly predicting the unlikely situation of an environment with no ant species, whereas the exponential model does not predict less than
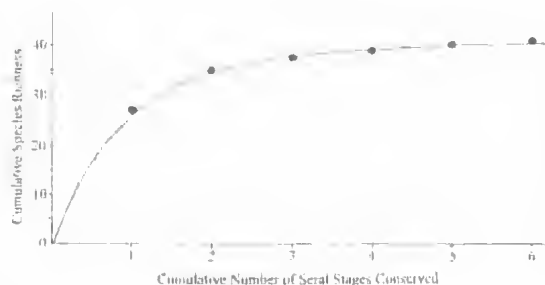
FIG. 3. Increase in total ant species richness with increasing number of habitats conserved.

one ant species for over 46 years after fire. Of the 20,000ha of open-forest in this area, only 3-4ha (0.02%) has remained unburnt for over 14 years. It is unlikely, therefore, that very old sites will persist in this environment, so the linear model would adequately describe the relationship for the most probable situation.

Changes in ant species richness over time at the control site show comparable trends to those described above (Fig. 2), with similar levels of variability (Table 1). Linear regression equations fitted to each data set independently have regression coefficients that are not significantly different ($F=2.62$ $DF=1,44$ $P=0.12$).

These results indicate there is a slow decline in ant species richness in the years after fire. The maintenance of high species diversity in a management context, however, must include not only a consideration of within-habitat (alpha) diversity, but also between-habitat (beta) diversity (MacArthur, 1965). In an area with a locally high fire frequency, the probability of a patch of forest remaining unburnt decreases with time since last fire, primarily due to the rapid accumulation of fuel (see Fox et al., 1979). If cumulative ant species richness is plotted against the cumulative number of patches of different ages (summed sequentially from youngest to oldest), the relationship takes the form of a species-area curve (Fig. 3). This frequently observed pattern may occur because there is an increase in environmental heterogeneity with increasing area sampled (Williams, 1964), thereby providing new micro-habitats and their component species; or might be related to the relative distribution of individuals among species (Preston, 1948, 1962, 1980), where the rarer species are more likely to be absent from small samples. An examination of the relative abundance distribution of the 41 ant species collected from these habitats (Fig. 4) indicates that rare species constitute the bulk of the ant 'biodiversity' at this scale. Nearly 60% of the species were found in less than 5% of the traps.

These 24 'rare' species are not concentrated in patches of a particular age since last fire (Fig. 5). The number of 'rare' species in any sub-plot is positively correlated with the total number of
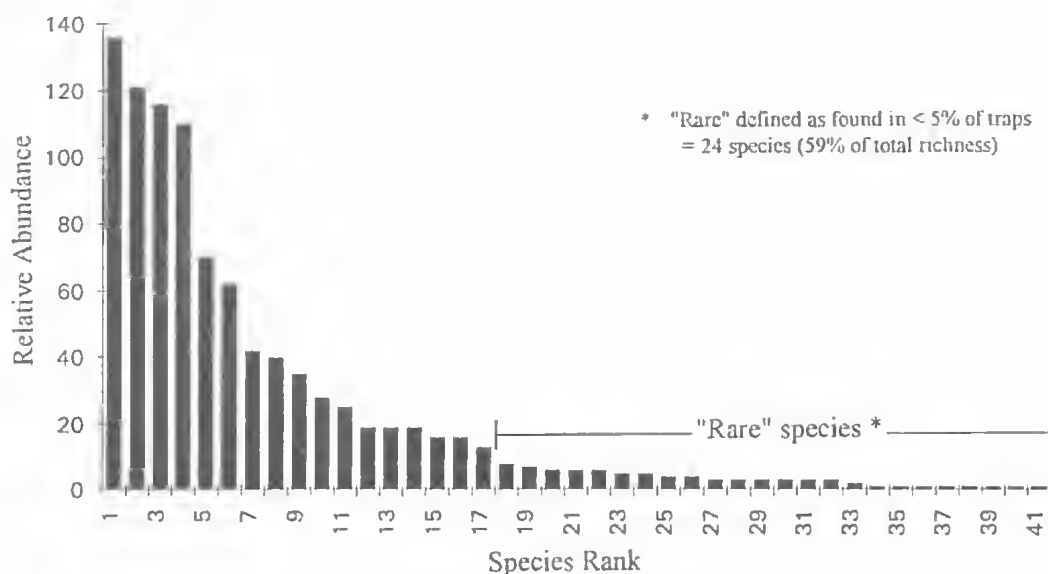

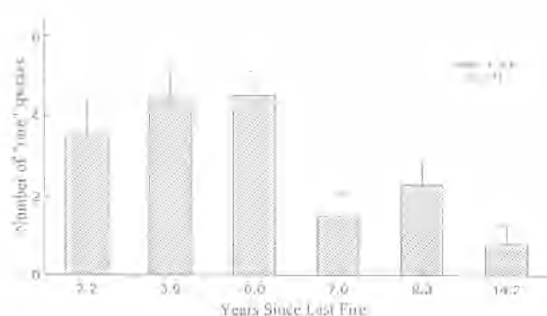FIG. 4. Forest ant community ranked species abundance.

FIG. 5. Distribution of species considered as 'rare' across sites differing in time since last fire.

species in that sample (r=0.766, n=24, P=0.00001). A closer examination of the distribution of rare species across age classes (Fig. 6) reveals three major patterns. Just under half (11) of these species are found only in one age class, namely: *Brachyponera lutea*, *Cerapachys* sp. A, *Hypoponera* sp. A, *Sphinctomyrmex steinheili*, *Cardiocondyla ?nuda*, *Colobostruma* sp. A, *Lordomyrma ?punctiventris*, *Monomorium* sp. B, *Doleromyrina darwiniana*, *Technomyrmex* sp. A and *Polyrhachis phryne*. Most of these were each found only at one sub-plot and were often represented by 1-2 individuals.

A further 8 species were found across a broad range of sub-plots, but again at low numbers. These species were: *Heteroponera imbellis*, *Aphaenogaster longiceps*, *Mayriella abstinens*, *Mesostruma browni*, *Strumigenys perplexa*, *Camponotus intrepidus*, *Camponotus myopores* and *Paratrechina minitula*. A third group of 5 species were more abundant but found only across ranges of plots of similar age. These species were: *Myrmecia gulosa*, *Mesoponera australis*, *Meranoplus* sp. A, *Myrmicina rugosa* and *Melophorus* sp. B.

DISCUSSION

In dry sclerophyll forest, fire is perhaps the most important natural source of disturbance. The inherent variability in natural fire regimes results in a mosaic of habitats with vegetation at different stages of floristic and structural post-fire succession. The importance of the structural complexity of the habitat in maintaining ant diversity has previously been reported (e.g. Brian et al., 1976; Boomsma & de Vries, 1980; Greenslade & Halliday, 1983; Andersen, 1986). Fire in this forest environment removes the bulk of understorey vegetation and initiates a pattern of structural habitat change (Fox et al., 1979; Fox, 1988). The

fact that most Australian ants nest are in the soil means they are largely protected from the immediate effects of fire (see Andersen & Yen, 1985; Neumann, 1992). Increases in ant abundance and species richness after fire have been reported, and burnt sites may still show significantly higher values than control plots 18 months after fire (Andersen, 1988).

This study has shown that, in the long-term, ant species richness declines after fire. Sixty-three percent of the variance in ant species richness was explained by a linear regression model with time since last fire as the independent variable. A model developed from chronosequence data predicted that by 7 years post fire, ant species richness would have decreased by 6 to 13 ($\pm$2.6) species. Species richness measured at a control site 7.2 years after fire was 13 ($\pm$1.3) species, lending strong support for the model in this forest environment. The richness of the ant community in the long-term is therefore strongly influenced by the fire interval (time since last fire), although the observed pattern could in part reflect a trapping artefact due to increasing habitat complexity over time (see Majer, 1980; Andersen, 1988).

The fire interval represents only one component of the fire regime (see Gill, 1975). However, it has a major effect on the forest community through fuel accumulation, which in turn influences fire intensity (Luke & McArthur, 1978). Although this research suggests that short fire intervals will maintain high ant species richness at a small scale, the management of biodiversity at a large scale must also consider the between-habitat (beta) diversity. Beta diversity is low in these forest habitats, with recently burnt sites supporting the bulk of the overall species richness.

An examination of the relative abundance of species, however, revealed that a substantial proportion (60%) of the overall richness was contributed by species which are uncommon or 'rare'. In studies of community ecology, rare species are often excluded from multivariate analyses because they contribute little to estimation of similarity or interpretation of pattern in the data. In this study, however, a considerable proportion of the overall biodiversity was contributed by these 'rare' or infrequently recorded species. These species were unevenly distributed amongst forest understorey age classes, with the number of 'rare' species being positively correlated with the overall richness at any particular sub-plot. Therefore, for a very high proportion

FIG. 6. Occurrence of 'rare' ant species at sites differing in time since last fire.

Subfamily Species	Years since last fire					
	2.2	3.9	6.0	7.0	8.3	14.2
Myrmeciinae						
Myrmecia gulosa	▬					
Ponerinae						
Brachyponera lutea		▬				
Cerapachys sp. A	▬					
Heteroponera imbellis	▬		▬			▬
Hypoponera sp. A				▬		
Mesoponera australis				▬		
Sphinctomyrmex steinheili					▬	
Myrmicinae						
Aphaenogaster longiceps		▬		▬		
Cardiocondyla ?nuda		▬				
Colobostruma sp. A	▬					
Lordomyrma ?punctiventris						▬
Mayriella (abstinens)	▬		▬			
Meranoplus sp. A	▬					
Mesostruma browni		▬				
Monomorium sp. B				▬		
Myrmicina rugosa			▬			
Strumigenys perplexa		▬		▬		
Dolichoderinae						
Doleromyrina darwiniana		▬				
Technomyrmex sp. A		▬				
Formicinae						
Camponotus (intrepidus)	▬		▬			
Camponotus (myopores)	▬				▬	
Melophorus sp. B	▬					
Paratrechina minitula	▬		▬			
Polyrhachis phryne	▬					
Total number of 'rare' species *	11	10	6	9	7	3
Number of unique 'rare' species	3	4	0	2	1	1

* 'rare' is defined as those species occurring in less than 5% of traps overall
( ) indicates likely species-group   *?* indicates most probable species identity

of species, there are insufficient data currently available to confidently predict their response to fire management strategies.

In the context of biodiversity conservation, these may be considered the species of greatest potential concern. While a number of these species showed no pattern as to their distribution — or were found in such low numbers that no conclusions could be drawn — the distribution of a number of species appeared to be linked with forest understorey age. Their rareness is unlikely therefore to reflect a sampling phenomenon but particular habitat conditions.

Some ant species have been shown to have flexible habitat requirements, while others are more specific (see Elmes, 1971; Levins et al., 1973; Chew, 1977; Doncaster, 1981; Majer et al., 1984). These results suggest that, as the habitat changes over time, there is a gradient over which the success, and hence relative abundance, of some species varies. In order to maintain viable populations of these species, and hence conserve them, these coastal forests need to be managed to preserve a mosaic of forest patches reflecting different times since last fire. The structure of these ant communities and the role of micro-habitat will need to be further explored in order to understand the conservation requirements of many of these rare species.

Increased utilisation of prescribed burning for conservation purposes has stimulated interest in prescribing 'natural fire season' burns and, in certain instances, a 'let-burn' strategy (Robbins & Myers, 1992) in which naturally ignited fires run their course. In many coastal forest environments in eastern Australia, high levels of human usage is leading to an increase in fire frequency and a reduction in the complexity of the understorey vegetation mosaic. This research has demonstrated that there is potential for a loss of species with this increasing habitat simplification. With the conservation of biodiversity being a fundamental part of 'multiple-use' forest management (Forest Use Working Group, 1991), fire prescriptions and fire control strategies must be designed to maintain the complexity of habitats on both small and large scales, and therefore maintain the high diversity of ant communities in these environments.

ACKNOWLEDGEMENTS

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